Seeing myself through my heart: cortical processing of a single heartbeat speeds up self-face recognition.

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ABSTRACT

Recent research has highlighted the contribution of interoceptive signals to different aspects of bodily self-consciousness (BSC) by means of the cardio-visual stimulation - i.e. perceiving a pulsing stimulus in synchrony with one's own heart. Here, for the first time, we investigate the effects of individual heartbeats on a critical feature of BSC, namely the recognition of one's own face. Across two studies, we explored the cardiac-timing effects on a classic self-face recognition task. In *Study 1*, participants saw morphed faces that contained different percentages of the self-face and that of another unfamiliar individual. *Study 2* used a similar design, albeit participants saw morphed faces of the self-face and that of a familiar other to provide a better control of self-familiarity. Results from both studies consistently revealed that the cortical processing of cardiac afferent signals conveyed by the firing of arterial baroreceptors affects the speed, but not the accuracy, of self-face recognition, when a single picture is presented during cardiac systole, as compared to diastole. This effect is stronger and **more** stable for stimuli with more self-cues than other-cues and for 'ambiguous' stimuli – i.e. at the individual point of subjective equality. Results from Study 2 also revealed that cardiac effects on the speed of self-face recognition cannot be explained simply on the basis of the imbalanced familiarity between the self's and other's faces used. The present findings highlight the interoceptive contributions to self-recognition and may be expand our understanding of pathological disturbances of self-experience.

KEYWORDS: Bodily Self; Face-Recognition; Cardiac Cycle Phases; Interoception.

1 INTRODUCTION

Bodily self-consciousness (BSC) is central to the sense of self (Blanke, 2012; Craig, 2002). **Recent studies have highlighted the contributions of both exteroceptive information (i.e., from the *outside* environment) and interoceptive signals (i.e., from *within* the body; (M. Tsakiris & De Preester, 2018)) and awareness to different aspects of BSC (Seth & Tsakiris, 2018). Specifically, these studies focused on body ownership (Suzuki, Garfinkel, Critchley, & Seth, 2013; Manos Tsakiris, Tajadura-Jiménez, & Costantini, 2011), self-location (Aspell et al., 2013; Park et al., 2016) and self-identification (Sel, Azevedo, & Tsakiris, 2017; Tajadura-Jimenez & Tsakiris, 2014). They used classic or modified versions of the Rubber Hand Illusion (RHI), the Full Body Illusion (FBI) and the Enfacement Illusion (EI), respectively, to investigate the role that interoceptive signals (e.g., cardiac) and their awareness may play in BSC, beyond exteroceptive information (e.g., visual, tactile).** Tsakiris, Tajadura and Costantini showed that the malleability of BSC, as studied with bodily illusions, depends on levels of interoceptive accuracy (IAcc; i.e., the ability to detect interoceptive signals, such as one's heartbeats); individuals with lower IAcc experience a stronger modulation of their BSC in the RHI (Manos Tsakiris et al., 2011) and the EI (Tajadura-Jimenez & Tsakiris, 2014). More recent studies have attempted to use interoceptive information as means of directly manipulating BSC. Suzuki and colleagues (Suzuki et al., 2013) applied cardio-visual stimulation to induce the RHI. They demonstrated that watching a virtual depiction of the participants' hand pulsing in synchrony, as opposed to out-of-synchrony, with their own heartbeats induced the illusory sense of ownership over the virtually projected hand. In particular, participants with higher IAcc experienced a stronger illusion than participants with lower IAcc. Analogously, Aspell and colleagues (Aspell et al., 2013) used the cardio-visual stimulation to induce the FBI. **They showed that watching a virtual projection of the participants' body surrounded by an illuminating silhouette flashing synchronously, as compared to asynchronously, with their own heartbeat led to enhanced self-identification, greater shift in self-location towards the virtual body and changes in tactile processing (see also (Heydrich et al., 2018) for follow-up).** More recently, Sel and colleagues (Sel et al., 2017) employed the cardio-visual stimulation to change the participants' mental representation of their face through the EI. They reported that perceiving a pulsing stimulus in synchrony

with one's own heart over a face containing only 60% of own-face features affects self-identification, through the incorporation of others' facial features into the mental representation of own-face. This was revealed by comparisons of participants' performance at self recognition task before and after the cardio-visual stimulation: participants accepted more facial features of the "other" in the morphed picture judged to equally represent "self" and "other" (i.e., point of subjective equality, PSE). Interestingly, this effect was stronger in participants with higher IAcc.

In sum, research on the effects of interoceptive signals on BSC has been so far entirely based on cardio-visual stimulation - i.e. perceiving a pulsing stimulus in synchrony with one's own heart over someone else's body/face for a short time interval. However, there is growing evidence that even the afferent signals at the level of individual heartbeats can influence perceptual (e.g., (Pramme, Larra, Schachinger, & Frings, 2014, 2016; Salomon et al., 2016)), cognitive (e.g., (Fiacconi, Peter, Owais, & Kohler, 2016; Garfinkel et al., 2013; Pfeifer et al., 2017)) and affective processing (e.g., (Azevedo, Badoud, & Tsakiris, 2017; Garfinkel et al., 2014)).

At each cardiac cycle, during the systolic phase (the ventricular ejection period in a cardiac cycle), the baroreceptors send a volley of afferent signals to the brainstem conveying information on strength and timing of individual heartbeats. These signals, which are of primary importance to the baroreflex control of blood pressure, are then forwarded to higher-order cortical structures including the amygdala, insula and cingulate cortex (see (Critchley & Harrison, 2013) for a review). By timing stimulus presentation to the maximal (systole), as opposite to the minimal (diastole), baroreceptor activity, it is possible to explore the impact of baroafferent signals on information processing. Depending on the stimulus category, context and task, baroafferent signals have been observed to modulate the salience of relevant stimulus cues. For instance, the detection and appraisal of disgusted (Gray et al., 2012) and fearful faces (Azevedo, Badoud, et al., 2017; Garfinkel et al., 2014) are enhanced when presented at systole relative to diastole. Moreover, it has been recently demonstrated that baroreceptor firing can modulate threat appraisal in context-dependent ways (Azevedo, Garfinkel, Critchley, & Tsakiris, 2017). On another line of research, studies have demonstrated that increased baroreceptor activity appears to improve visual selection efficiency (Pramme

et al., 2014, 2016), possibly due to enhancement of inhibitory processes needed to solve perceptual interference (Pramme et al., 2016). The extent to which such effects of cardiac cycle can apply to self-related processing, such as the recognition of one's own face, remains unknown.

Here, we hypothesize that baroreceptors signals may enhance the salience of self-cues during self-face recognition, and test this hypothesis in two studies. *Study 1* explored cardiac-timing effects on a classic self-face recognition task (Keenan et al., 1999) where participants saw morphed faces that contained different percentages of the self-face and that of another unfamiliar gender-matched individual. *Study 2* used a similar design, albeit participants saw morphed faces of the self-face and that of a familiar other to provide a better control of self-familiarity. For each study, we estimated and compared both individual PSEs and reaction times (RTs), for stimuli presented at systole or at diastole. Cardiac cycle effects on PSEs would suggest that baroafferent information induces a shift in self-face representation, as in the cardio-visual illusion (Sel et al., 2017), while significant effects on RTs would indicate that the same information speeds up processing of self-cues leading to self-recognition.

2. STUDY 1

2.1 SELF-RECOGNITION TASK (self face-unfamiliar face)

In order to explore cardiac-timing effects on the processing of one's own face, and their possible relation with individual interoceptive accuracy, each participant in Study 1 performed both a Self-recognition task and a Heartbeat Perception Task (Schandry, 1981).

2.1.1 MATERIALS AND METHODS

2.1.1.1 Participants

A total of 32 healthy individuals (18 females, 14 males; mean age = 22 years, *SD* = 3 years) participated in the study, after giving written informed consent. Three additional participants were excluded due to incorrect interpretation of the instructions or bad fitting results. A sensitivity analysis revealed that our sample size was large enough to detect a significant within-subjects effect corresponding to a medium

effect size (Cohen's *d* = .5; as far as we are aware, formal analysis methods have not been developed that are adequate to precisely compute statistical power for the mixed-effects models we performed here). All participants had normal or corrected to normal vision. The study was approved by the Department of Psychology Ethics Committee, University of Essex. Participants received an expense allowance of £8 or partial course credit for their participation.

2.1.1.2 Stimuli.

Stimuli used during the Self-Recognition Task consisted of photos of the participant's face ("Self") morphed with a gender-matched unfamiliar face ("Unfamiliar Other"). Participants' pictures were taken before the experiment. Participants were instructed to look directly into the camera with a neutral expression. The photos were then processed in GNU Image Manipulation Program (GIMP, https://www.gimp.org/). In accordance with previous studies (e.g. Chakraborty & Chakrabarti, 2015; Sel, Azevedo, & Tsakiris, 2018), these non-mirror reversed photos were desaturated (i.e. converted in grayscale) and cropped to an oval frame stretching from ear to ear, below the hairline to the chin, in order to remove non-facial features (e.g., ears and hairs). For each participant, the unfamiliar face was randomly selected from our in-house database, which included 70 models (46 females, 29 males) that had never been seen by the participants before the experiment. Morphed stimuli ranging from 0% morphing (100% Self-0% Other) to 100% morphing (0% Self-100% Other) were produced using SmartMorph (V.1.55 http://meesoft.logicnet.dk/). Nine degrees of morphing were selected for the Self-recognition task (% of self): 0, 20, 35, 45, 50, 55, 65, 80, and 100 (Figure 1a). All images were presented on a black background using a cathode ray tube monitor at an approximate distance of 55 cm. Stimulus presentation and participants' responses were controlled by a PC running Matlab Psychtoolbox (Brainard & Brainard, 1997; Kleiner et al., 2007).

2.1.1.3 Experimental design and Procedure.

Unbeknown to the participants, morphed stimuli were presented with timings that allowed synchronization with the cardiac cycle (i.e. systole or diastole). To this purpose, three pre-gelled ECG electrodes (Ag/AgCI)

were placed in a III-Lead chest configuration: two electrodes were positioned underneath the left and right collarbone, and another one on the participant's lower abdomen on the left side. The cardiac signal was recorded continuously with a BioPac ECG100C Electrocardiogram Amplifier (band-pass filter: .5-35 Hz; sampling rate: 500 Hz) using the AcqKnowledge software. The R-peaks were identified online by detecting when the amplitude of the signal exceeded an individually defined threshold. The threshold was set by the experimenter by visually inspecting the ECG trace prior to the testing phase. Morphed stimuli were presented either within the participant's cardiac systole (Systole condition), which is the period of maximal representation of baroreceptor afferent information, or within the cardiac diastole (Diastole condition), the remaining period of the cardiac cycle. According to previous studies, the systolic period was defined as 200-400 ms and the diastole as 400-800 ms after the R-peak of the QRS complex (e.g., Garfinkel, Critchley, Tsakiris, & Azevedo, 2017; Kroeker & Wood, 1955). In particular, once the pulse pressure wave reaches the aortic arch, the arterial baroceptors that carry the cardiac information to the brain start firing with a maximum peak estimated at R+250 ms (Edwards, Ring, McIntyre, Winer, & Martin, 2009; James, 1971). Accordingly, in the Systole condition (stimuli time locked to the cardiac systole) pictures were presented at R+200 ms, whereas in the Diastole condition (stimuli time locked to diastole), the pictures were presented at R+500 ms (Figure 1b). Control analyses confirmed that our procedure ensured the desired timing of stimuli presentation with a good accuracy and precision. The average (SD) actual delay between the R peak and the onset of the stimuli, as measured by timestamps, was 207 ms (1 ms) and 507 ms (2 ms) for the Systole and Diastole conditions, respectively.

Participants were seated in a dimly lit, sound-attenuated room. They were presented with a pseudo-randomized series of photos reflecting different degrees of self-other morphing (% of self): 0, 20, 35, 45, 50, 55, 65, 80, and 100 (Figure 1a). Each trial started with a fixation cross presented at the centre of the screen until the next R-peak was detected. After either 200 ms (Systole condition) or 500 ms (Diastole condition) from the R-peak detection, a morphed face was presented for 250 ms (Figure 1b). This allowed us to investigate the effects of baroreceptor activity on self-recognition. Participants were then prompted to provide an answer within the following 1500 ms. If no answer was provided, the picture was presented

again at the end of experimental block. The inter-trial interval was jittered between 1500 and 2500 ms. At the end of each block, participants rested for at least one minute. The entire task consisted of four blocks (two Systole and two Diastole blocks). The order of the blocks was randomized across participants. In each block, each stimulus was presented 10 times, for a total of 90 stimuli per block. Within blocks, stimuli were presented in a pseudo-randomized order. Participants were asked to pay attention to the face stimuli presented on the computer screen and judge whether the face belonged to themselves, or to someone else, by pressing one of two keys on a computer keyboard ("S" or "L"). Participant's answers and reaction times were recorded. The Self-Recognition Task was preceded by a training phase comprising 9 stimuli, one for each morphing degree.

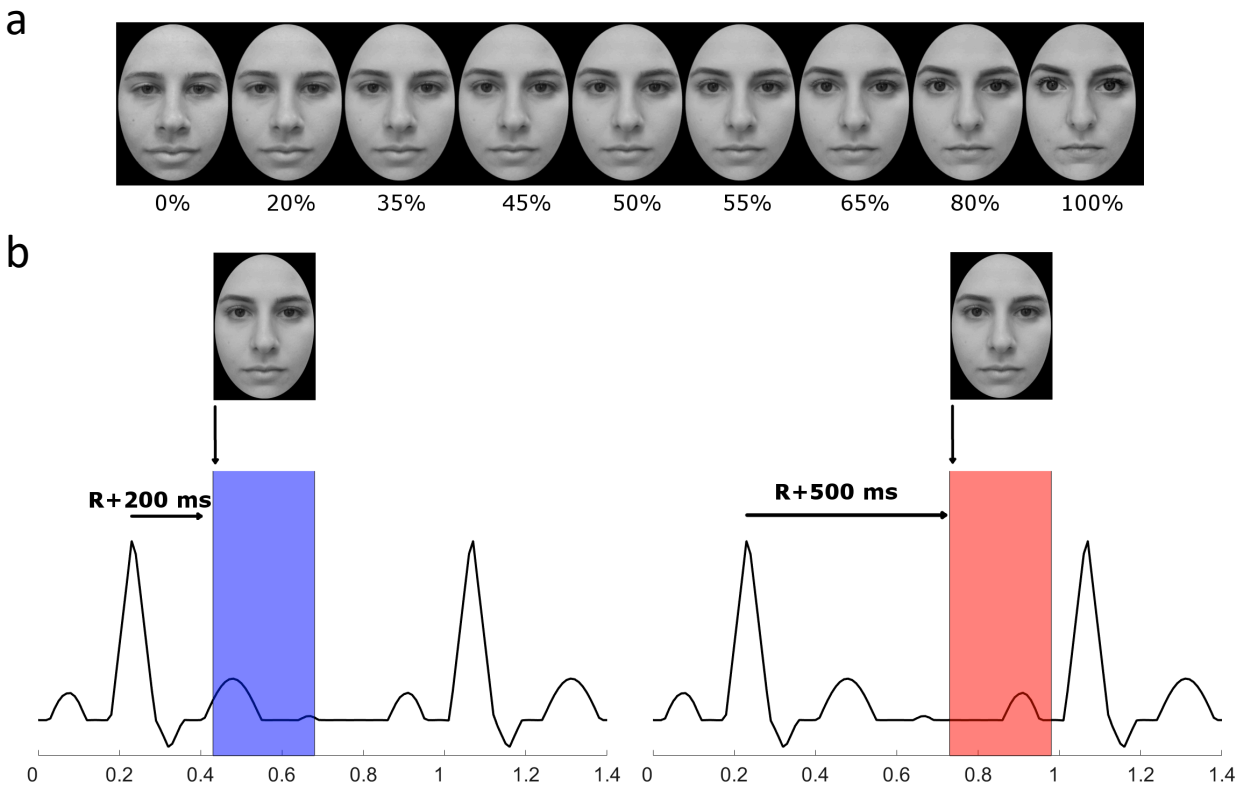

Figure 1. Stimuli and timing of cardio-visual stimulation
a) Example of a participant's face (0%) morphed in nine steps with an unknown, same-gender face (100%) resulting in seven degrees of morphing between the two faces, with increasing % of Self. b) Presentation of stimuli during the cardiac systole in the Systole condition (left panel) and during the cardiac diastole in the Diastole condition (right panel). Two exemplar cardiac cycles are shown in each panel, with the semi-transparent rectangles indicating onset and duration of the stimulus presentation.

2.1.1.4 Data analysis

Self-other judgment probabilities. Our first analysis was aimed at assessing changes in the representation of self-other faces due to cardiac afferent signals as measured by differences in participants' psychometric function of self-other judgments. To this aim, we first calculated the participant's proportion of 'other' responses for each cardiac cycle phase (i.e., Systole and Diastole) and level of morphing (i.e., 0, 20, 35, 45, 50, 55, 65, 80, and 100). Next, we checked whether participants showed perfect accuracy in discriminating non-morphed faces, that is, the stimuli corresponding to the morphing levels 0 (i.e, the self-face) and 100 (i.e., the other face), respectively. To this end, we conducted two one-tailed one-sample t-tests, against 0 and 1, respectively, on participants' proportion of 'other' responses for non-morphed self and other faces. This analysis revealed that participants showed non-perfect accuracy in discriminating non-morphed faces (all $|t| > 2.72$, all $p < .003$, all $d > .48$), with a proportion of errors that was significantly higher than 0. We then fitted the individual self-other probabilities for each condition by using the four-parameter logistic function (Pmin+Pmax)/{1+exp[-(b0+b1*x)]}, where x indicates the morphing level, b0 and b1 are the two parameters of the standard logistic function, and Pmin and Pmax are two additional parameters denoting, respectively, the lower and upper asymptote to which the logistic function was limited. The Pmin and Pmax parameters thus reflect the general error in discriminating non-morphed self and other stimuli, respectively. The logistic functions were fitted by using in-house functions written in Matlab, which employed an iterative procedure to accurately estimate the four parameters. Based on the fitted psychometric curves, we estimated the Point of Subjective Equality (PSE) as the morphing level where the curve crossed the 50% probability of 'other' responses. This measure reflects the participant's degree of bias in self-other judgments, with values lower and higher than 50 reflecting a bias towards reporting self and other faces, respectively. We also computed a value corresponding to the so-called Just Noticeable Difference (JND) as the difference between the morphing levels where the curve crossed the 75% and 25% probability of 'other' responses. This measure reflects the participant's precision in self-other judgments, with lower values denoting a steeper psychometric function and, thus, a more abrupt transition from 'self' to 'other' predominant responses.

Finally, in order to assess changes in the representation of self-other faces due to cardiac afferent signals, we compared participants' PSE and JND values in Systole and Diastole conditions by means of two-tailed paired-sample t-tests. These measures were also submitted to a correlation analysis along with the individuals' IAcc scores to investigate whether, and to what degree, the latter measure may contribute to explain inter-individual variability in self-other representations. Specifically, we calculated Pearson's correlations and performed null hypothesis statistical significance testing using the nonparametric percentile bootstrap test (2000 resamples; two-sided 95% confidence interval, $_{95\%}$CI, corresponding to an α level of 0.05), which is more robust than the traditional t-test against heteroscedasticity (Pernet, Wilcox, & Rousselet, 2012).

Response times. In a second analysis, we assessed whether cardiac afferent signals affected the time required to complete the decision processes leading to self-other judgments accounting for the individual differences in the subjective perception of self-other faces, as indexed by the PSE. To this aim, response times (RTs) were first log-transformed (lnRTs). Next, for each participant, we 'scaled' each morphing level so to obtain the individual, subjective amount of evidence for self vs. other relative to the individual PSE. We labelled this measure as 'relative' morphing level. Specifically, we subtracted the individual PSE for each cardiac cycle phase (i.e., Systole and Diastole) from the morphing level (which varied from 0 to 100), thus obtaining an individual, continuous measure of deviation from PSE that ranged from 0 – PSE to 100 – PSE and took negative values for stimuli perceived as self, a value of 0 for the PSE, and positive values for stimuli perceived as other. Moreover, since we expected the self and other stimuli to have a different effect on decision processes, we added a categorical factor accounting for the type of stimulus relative to the individual PSE (see (Sedda et al., 2018)); this independent variable 'StimType' was obtained by coding negative PSE-scaled morphing level as self and positive ones as other. As these latter independent variables were condition- and participant-dependent, we assessed the effects of our experimental manipulations on the trial-level lnRTs by using a linear mixed-effect model analysis as implemented by the function *lmer* from the lme4 library (Bates, Mächler, Bolker, & Walker, 2015) in R (version 3.3.3; (RCoreTeam, 2017)). Indeed,

one of the advantages of mixed-effects modelling that makes it particularly appropriate in our case is that it easily allows to test for the effect of individual-dependent continuous predictors (and their interactions with categorical ones), usually with a gain in statistical power (Kliegl, Wei, Dambacher, Yan, & Zhou, 2010). A further advantage of this statistical approach is that it allows controlling for longitudinal effects during the task such as the effects of fatigue and learning (Baayen, Davidson, & Bates, 2008). The appropriate (final) linear mixed-effect model to fit participants' lnRTs was determined by using log-likelihood ratio test according to standard procedures (e.g., (Baayen et al., 2008; Bates et al., 2015; Quené & van den Bergh, 2008); for a detailed description of the procedure, see (Montefinese, Zannino, & Ambrosini, 2015); see also (Ambrosini, Pezzulo, & Costantini, 2015)). The final model included three parameters for the fixed effects of the confounding variables Block and Trial order, as well as their interaction, which account for longitudinal effects during the task. The final model also included, in the fixed part, the parameters for the main effects and interactions involving the independent variables of interest, that is, the CardiacCycle factor (Systole vs. Diastole), the stimulus type factor (StimType: self vs. other), the continuous predictor relative morphing level (relMorphing, see above). A random intercept varying among participants (SSid), as well random slopes for Block and Trial order and their interaction were entered into the model as random effects. The R-notation formula of the final model is *lnRT ~ Block*Trial + CardiacCycle + relMorphing + relMorphing:StimType + relMorphing:CardiacCycle + relMorphing:StimType:CardiacCycle + (1|SSid) + (0 + Block*Trial|SSid)*. Note that the model did not include the main effect of StimType in order to ensure the equivalence of lnRTs at the PSE (i.e., the relMorphing value of 0) and, thus, to avoid discontinuity of the model around the PSE (note that real data do not show discontinuity, or an abrupt change in performance, at the PSE). In order to facilitate the convergence of the models, the variables were centered and/or scaled. The final model was re-fitted after excluding observations with absolute standard residuals greater than 2 (5.4%). The statistical significance of predictors was assessed by means of t tests with Satterthwaite's approximation to degrees of freedom provided by the *lmerTest* package. We report the estimated coefficient (*b*), standard error (*SE*), *t* and *p* values for each parameter included in the final model.

2.2 HEARTBEAT PERCEPTION TASK

To assess interoceptive accuracy, we used the Mental Tracking Method (Schandry, 1981). **All participants performed this task after the self-recognition task.** In twelve trials, participants silently counted how many heartbeats they felt over varying time intervals (three 25-s trials, three 35-s trials, three 45-s trials, three 100-s trials), randomly presented. They were instructed to count their heartbeats without taking their pulse. Responses were then compared with how many heartbeats were measured by ECG. ECG traces were analysed using in-house scripts written in Matlab. R-peaks were identified with a semi-automatic procedure and checked visually. The individual interoceptive accuracy (IAcc) was then calculated as the mean score of the heartbeat perception trials (Schandry, 1981): Σ(1 − (|recorded heartbeats − counted heartbeats| / recorded heartbeats))/12. Thus, IAcc values varied between 0 and 1, with higher scores indicating better interoceptive accuracy.

2.3 RESULTS

2.3.1 Self-other judgment probabilities

The four-parameter logistic function fitted participants' self-other judgments adequately, as evidenced by the high R^2 values for both Systole and Diastole conditions (respectively, M = .990 and .991, SD = .010 and .012). A two-tailed paired-sample t-test on the PSE (i.e., the degree of bias in self-other judgments) did not reveal any significant difference between Systole and Diastole conditions ($t_{(31)}$ = .34, p = .735, d = .06). Two-tailed one-sample t-tests revealed that participants' exhibited a significant bias toward judging the stimuli as self in both conditions, as shown by the fact that mean PSE values were significantly lower than the 50% morphing level (Systole: M = 44.48, SD = 10.59, $t_{(31)}$ = -2.95, p = .006, d = -.52; Diastole: M = 44.71, SD = 10.91, $t_{(31)}$ = -2.74, p = .010, d = -.49). The analysis performed on JND values also revealed no significant effect of our experimental manipulation ($t_{(31)}$ = .22, p = .830, d = .04), with similar precision in self-other judgments between Systole (M = 13.29, SD = 7.31) and Diastole (M = 13.60, SD = 9.83) conditions. Figure 2a shows the psychometric functions aggregated across participants in the Systole (blue lines) and Diastole (red lines) conditions.

Additional control analyses revealed that the participants' values of the Pmin parameter for the Systole and Diastole conditions were both significantly higher than 0 (respectively, *M* = .044 and .035, *SD* = .062 and .064, $t_{(31)}$ = 4.01 and 3.05, *p* = .0004 and .005, *d* = .71 and .54) and did not differ between each other ($t_{(31)}$ = -1.23, *p* = .226, *d* = -.22). Similarly, participants' values of the Pmax parameter for the Systole and Diastole conditions were both significantly lower than 1 (respectively, *M* = .950 and .953, *SD* = .069 and .077, $t_{(31)}$ = -4.14 and 3.49, *p* = .0002 and .001, *d* = -.73 and -.62) and did not differ between each other ($t_{(31)}$ = .24, *p* = .810, *d* = .04).

Correlation analyses revealed that participants' IAcc scores were significantly correlated to their PSE values in both the Diastole (*r* = .33, $_{95\%}$CI = [.01 .55]) and Systole (*r* = .39, $_{95\%}$CI = [.07 .60]) conditions: participants with higher IAcc values tended to have higher PSE values or, in other words, to have a bias toward judging the stimuli as self (Figure 2 c,d). Conversely, no significant correlation was found between participants' IAcc and their JND values in either the Diastole (*r* = -.01, $_{95\%}$CI = [-.22 .39]) or the Systole (*r* = .09, $_{95\%}$CI = [-.42 .26]) condition.

2.3.2 Response times

The results of the linear mixed-effects analysis on the lnRTs are shown in Table 1. The analysis revealed the significance of all the effects except that of the relMorphing by CardiacCycle interaction. In particular, the significant effects of Trial and Block factors show that participants' RTs became faster as the experiment went on, as indicated by the negative sign of each factor's parameter (see Table 1). This holds true especially in the first blocks, as indicated by the interaction Trial:Block and the positive sign of its parameter (see Table 1). Moreover, the significant CardiacCycle main effect shows that participants were slower in giving their judgments when the stimuli were presented during their cardiac diastole as compared to the systole. Of particular interest for our hypothesis, the remaining effects indicate that it took more time for participants to discriminate between self and other faces as they were closer to their subjective PSE values (as evidenced by the significant effect of relMorphing and its interaction with the StimType factor) and that the Diastole – Systole difference in lnRTs (i.e., the 'Diastole cost') became smaller as more evidence was available (i.e., as the relMorphing values became larger in absolute terms), especially for other faces (see

Figure 2b). To better understand this higher-order interaction, we performed two follow-up analyses on the data for the self and other sides of the stimuli space separately (i.e., on the data for the "self" and "other" levels of the StimType factor, respectively, while keeping all the other factors as in the main final model). These analyses revealed that the Diastole cost was significant but stable across the relMorphing levels for the self stimuli (as evidenced by the significant CardiacCycle effect and the non-significant relMorphing by CardiacCycle interaction), whereas it became smaller as more evidence was available for the other stimuli, that is, as the stimulus was more clearly another's face (as evidenced by the interaction between the CardiacCycle and the relMorphing variables). In summary, Study 1 showed that baro-afferent signals affect the speed, but not the accuracy, of self-face recognition, when a single picture is presented during cardiac systole, as compared to diastole. This effect on RTs is stronger and **more** stable for stimuli with more self-cues than other-cues and for "ambiguous" stimuli (at PSE), while it decreases as the proportion of other-cues increases.

Table 1. Estimated parameters and statistics of linear mixed-effects modelling of response times in Study

Fixed effects	***B***	***SE***	***T***	***P***
(Intercept)	6.595	.025	264.00	<.001
Block	-.036	.006	-6.01	<.001
Trial	-.006	.003	-2.25	.032
Trial:Block	.007	.003	2.82	.008
CardiacCycle $_{(Diastole)}$	.033	.006	5.75	<.001
relMorphing	.082	.003	26.98	<.001
relMorphing: CardiacCycle	.006	.004	1.53	.127
relMorphing:StimType$_{(Other)}$	-.162	.005	-34.42	<.001
relMorphing:StimType: CardiacCycle	-.018	.007	-2.71	.007

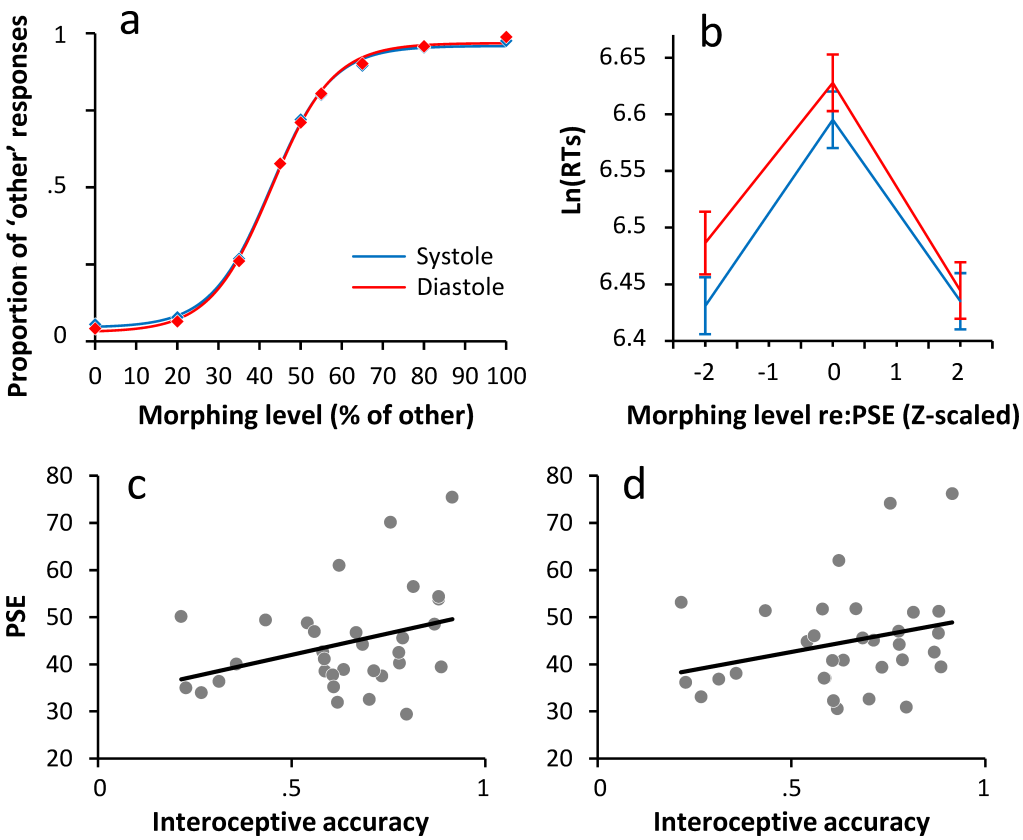

Figure 2. Study 1: results.
a) Psychometric functions aggregated across participants in the Systole (blue line) and Diastole (red line) conditions. Blue and red points indicate the corresponding mean percentage of 'other' responses. b) Results of the linear mixed-effect analyses on lnRTs. The figure shows the relMorphing:StimType: CardiacCycle interaction. The fitted lnRTs are plotted as a function of the Z-scaled stimulus morphing level relative to the individual PSE (x axis) for the Systole (blue line) and Diastole (red line) conditions. c,d) correlation between Interoceptive accuracy and individual PSE at Systole (c) and Diastole (d) conditions.

3. STUDY 2

3.1 SELF-RECOGNITION TASK (self face- familiar face)

This study aimed at providing an internal replication and also at controlling for face familiarity to rule out the possibility that the cardiac-timing effects on self-recognition that were observed in Study 1 could be explained simply on the basis of the imbalanced familiarity between the self's and other's faces used. To this aim, we asked a new group of participants to perform the Self-recognition task with stimuli depicting their face morphed with highly familiar faces of famous persons.

3.1.1 MATERIALS AND METHODS

3.1.1.1 Participants

A total of 37 individuals participated in the study (14 females, 23 males; mean age = 20 years, *SD* = 2 years). Three additional participants were excluded due to incorrect interpretation of the instructions or bad fitting results. A sensitivity analysis revealed that our sample size was large enough to detect a significant within-subjects effect corresponding to a medium effect size (Cohen's *d* = .5; as far as we are aware, formal analysis methods have not been developed that are adequate to precisely compute statistical power for the mixed-effects models we performed here). All participants had normal or corrected to normal vision. The study was approved by the Department of Psychology Ethics Committee, University of Essex. Participants received an expense allowance of £8 or partial course credit for their participation.

3.1.1.2 Stimuli

Stimuli used in this study consisted of photos of the participant's face ("Self") morphed with a gender-matched famous person's face that was highly familiar to the participants ("Familiar Other"). Photos of famous faces were taken from the Internet forming a database of 84 models (46 males and 38 females). To make sure that participants chose the famous person's face based on familiarity, rather than self-resemblance, we asked them to look at the database and indicate the famous face that was the most familiar to them and that they identified with the most, and then the famous face that was the most familiar to them and that they identified with the least (see *Supplemental material*). The photo selected by the participant as the famous person that they identified with the least was used as "Familiar Other" in the Self-Recognition Task. Photo editing, production of morphed stimuli and stimulus presentation were the same as in Study 1.

3.1.1.3 Experimental design and Procedure.

Same as in Study 1.

3.1.1.4 Data analysis.

Same as in Study 1 except that, when applying linear mixed-effect model to fit participants' lnRTs, 5.6% of the observations with absolute standard residuals greater than 2 were excluded before the final model was re-fitted.

3.2 RESULTS

3.2.1 Self-other judgments probabilities.

As expected, the results were similar to those observed in Study 1. The four-parameter logistic function fitted participants' self-other judgments adequately, with high R^2 values for both Systole and Diastole conditions (respectively, M = .991 and .995, SD = .018 and .006). A two-tailed paired-sample t-test on the PSE did not reveal any significant difference between Systole and Diastole conditions ($t_{(36)}$ = .87, p = .389, d = .14). The two-tailed one-sample t-tests revealed that participants' exhibited a significant bias toward judging the stimuli as self in both conditions, as shown by PSE values that were significantly lower than the 50% morphing level (Systole: M = 39.29, SD = 12.21, $t_{(36)}$ = -5.34, p < .0001, d = -.88; Diastole: M = 39.89, SD = 10.36, $t_{(31)}$ = -5.93, p < .0001, d = -.98). The analysis performed on JND values also revealed no significant effect of the CardiacCycle ($t_{(36)}$ = -1.82, p = .076, d = -.30), with similar precision in self-other judgments between Systole (M = 6.06, SD = 3.23) and Diastole (M = 5.42, SD = 3.27) conditions. Figure 3a shows the psychometric functions aggregated across participants in the Systole (blue lines) and Diastole (red lines) conditions. Additional control analyses confirmed that the participants' Pmin values for the Systole and Diastole conditions were both significantly higher than 0 (respectively, M = .038 and .031, SD = .053 and .044, $t_{(36)}$ = 4.35 and 4.25, p = .0001 and .0001, d = .72 and .70) and did not differ between each other ($t_{(36)}$ = -1.18, p = .244, d = -.19). Similarly, participants' values of the Pmax parameter for the Systole and Diastole conditions were both significantly lower than 1 (respectively, M = .950 and .958, SD = .067 and .047, $t_{(36)}$ = -4.59 and 5.42, p = .0001 and .0001, d = -.75 and -.89) and did not differ between each other ($t_{(36)}$ = 1.01, p = .320, d = .17).

3.2.2 Response times

The results of the linear mixed-effects analysis on the lnRTs are shown in Table 2. The analysis revealed the significance of all the effects except that of the relMorphing by CardiacCycle interaction. In particular, the significant effects of Trial and Block factors show that participants' RTs became faster as the experiment went on, as indicated by the negative sign of each factor's parameter (see Table 2). This holds true especially in the first blocks, as indicated by the interaction Trial:Block and the positive sign of its parameter (see Table 2). Moreover, the significant CardiacCycle main effect shows that participants were slower in giving their judgments when the stimuli were presented during their cardiac diastole as compared to the systole. Again, the remaining effects indicate that it took more time for participants to discriminate between self and other faces as they were closer to their subjective PSE values (as evidenced by the significant effect of relMorphing and its interaction with the StimType factor) and that the Diastole cost became smaller as more evidence was available, especially for other faces (see Figure 3b). To better understand this higher-order interaction, we performed two follow-up analyses on the data for the self and other sides of the stimuli space separately (i.e., on the data for the "self" and "other" levels of the StimType factor, respectively, while keeping all the other factors as in the main final model). As in Study 1, the analyses on the self stimuli revealed that the Diastole – Systole difference in lnRTs was significant but stable across the relMorphing levels for the self stimuli. In other words, the red line on the left side ('self' side) of Figure 3b is statistically higher than the blue one, but their slopes are not statistically different (as evidenced by the significant CardiacCycle effect and the non-significant relMorphing by CardiacCycle interaction). By contrast, and as in Study 1, the analyses on other stimuli revealed that the Diastole – Systole difference in lnRTs was significant at the PSE (as revealed by the significant main effect of CardiacCycle), but it became smaller as more evidence was available for the other stimuli, that is, as the stimulus was more clearly an other face. In other words, the red line on the right side ('other' side) of Figure 3b is statistically higher than the blue one at the PSE, but its slope is steeper than the blue one, so

the red – blue difference becomes smaller for higher relMorphing values (as evidenced by the significant interaction between the CardiacCycle and the relMorphing variables).

Table 2. Estimated parameters and statistics of linear mixed-effects modelling of response times in Study 2

Fixed effects	*B*	*SE*	*T*	*p*
(Intercept)	6.623	.020	323.66	<.001
Block	-.048	.006	-8.41	<.001
Trial	-.009	.002	-4.00	<.001
Trial:Block	.006	.002	3.13	.003
CardiacCycle $_{(Diastole)}$	.019	.005	3.72	<.001
relMorphing	.087	.003	28.34	<.001
relMorphing: CardiacCycle	-.001	.004	-.21	.831
relMorphing:StimType$_{(Other)}$	-.171	.004	-38.58	<.001
relMorphing:StimType:CardiacCycle	-.013	.006	-2.04	.041

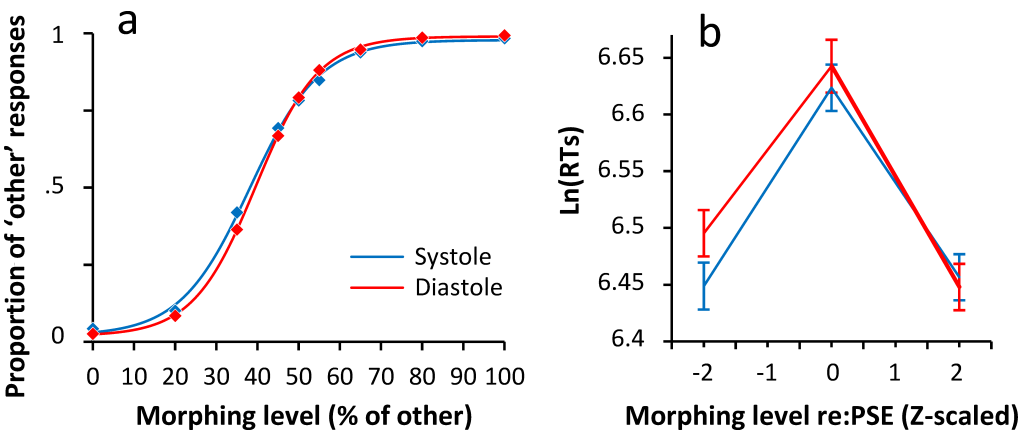

Figure 3. Study 2: results.

a) Psychometric functions aggregated across participants in the Systole (blue line) and Diastole (red line) conditions. Blue and red points indicate the corresponding mean percentage of 'other' responses. b) Results of the linear mixed-effect analyses on lnRTs. The figure shows the relMorphing:StimType: CardiacCycle interaction. The fitted lnRTs are plotted as a function of the Z-scaled stimulus morphing level relative to the individual PSE (x axis) for the Systole (blue line) and Diastole (red line) conditions.

3.2.3 Between-study analysis.

In order to confirm that these results were consistent with those observed in Study 1, we carried out a between-study analysis on lnRTs by testing a linear mixed-effects model including the main effect of the Study factor (Study 1 vs. 2) and the corresponding interactions. The results of this analysis are shown in Table 3. The between-study analysis confirmed the results observed in both studies and, most importantly, suggests that the results were not modulated by the Study factor, as the effects involving this factor were all non-significant.

In summary, Study 2 first showed that cardiac effect on the speed of self-face recognition cannot be explained simply on the basis of the imbalanced familiarity between the self's and other's faces used. Second, as proved by the between-study analysis, it fully replicated results from Study 1.

Table 3. Estimated parameters and statistics of the between-study linear mixed-effects model on response times

Fixed effects	*B*	*SE*	*t*	*P*
(Intercept)	6.595	.023	281.39	< .001
Block	-.043	.004	-10.17	< .001
Trial	-.007	.002	-4.42	< .001
Trial:Block	.007	.002	4.22	< .001
$Study_{(2)}$	.028	.032	.88	.384
$CardiacCycle_{(Diastole)}$	.033	.006	5.77	< .001
relMorphing	.082	.003	27.18	< .001
relMorphing:CardiacCycle	.007	.004	1.56	.118
$relMorphing:StimType_{(Other)}$	-.163	.005	-34.67	< .001
relMorphing:StimType:CardiacCycle	-.018	.007	-2.74	.006
Study:CardiacCycle	-.013	.008	-1.73	.084
Study:relMorphing	.005	.004	1.19	.234
Study:relMorphing:CardiacCycle	-.007	.006	-1.21	.225
Study:relMorphing:StimType	-.008	.006	-1.29	.196
Study:relMorphing:StimType:CardiacCycle	.005	.009	.52	.601

4. DISCUSSION

We investigated the effects of individual heartbeats on a critical feature of BSC, namely the recognition of one's own face. Across two studies, we showed that self-face recognition is at least partly modulated by the cortical processing of cardiac afferent signals conveyed by the firing of arterial baroreceptors. Results from both studies revealed for the first time that presenting a single picture in synchrony with the participant's heartbeat affects the speed of self-face processing. Faster RTs for stimuli presented during cardiac systole, as compared to diastole, clearly indicated that baroafferent information speeds up processing of self-cues leading to self-recognition. More specifically, participants were faster to discriminate between self and other faces during cardiac systole, as compared to diastole, especially for faces that were judged as self and at "more ambiguous" conditions, i.e. as participants were closer to their subjective PSE values. This difference became smaller as more evidence was available for other faces, thus, suggesting stronger cardiac effect on the processing of self-cues than other-cues. Moreover, results from Study 2 and the between-study analysis proved that cardiac effects on the time required to complete the decision processes leading to self-other judgments cannot be simply explained by familiarity of self-images. Beyond the effects on RTs, we did not observe any significant effects on accuracy as a function of cardiac cycle. Estimations of both self-bias, as indexed by the PSE, and precision in self-other judgments, as indexed by the JND, were not significantly different for images presented at systole relative to diastole. Accordingly, we did not find any specific effect of individual trait levels IAcc on the processing of images presented at systole. Rather, in Study 1, we observed a general linear increase in self-bias (PSE) with IAcc, for both Systole and Diastole conditions. In sum, our results show that single picture presentation synchronized with the participant's heartbeat speeds up self-face recognition, while it does not affect self-identification with the face of another, unlike the continuous synchronous cardio-visual stimulation leading to the enfacement illusion (Sel et al., 2017), which however was not the target of our studies.

The fact that we observed stronger cardiac effects as the proportion of self-cues in the image increased might be consistent with the idea proposed by Sui & Humphreys (2017) that, especially when self-related stimuli are being perceived and processed, the self acts as a stable anchor in decision making. Moreover,

it has been suggested that the default mode of processing of the social brain is to process self-related information (Bird & Viding, 2014), and what our two experiments suggest is that the concurrent cortical representation of cardiac signals with self-related visual information facilitates, at least in speed, the recognition of one's own face. Cardiac afferent signals may enhance in a general fashion the salience of self-cues, as they convey information about internal bodily states, which set the foundations for a sense of self (Craig, 2002, 2003). As a result, a certain proportion of self-cues must be present in morphed images in order for cardiac signals to facilitate self-other judgments. Importantly, we observed larger differences between the speed of self-other judgments at systole, as compared to diastole, for ambiguous stimuli (i.e. close to the PSE) and when the ambiguity (i.e., the amount of morphing) was added to the self face; conversely, this systole-related effect on RTs was strongly reduced as the stimulus was more clearly the face of another (i.e. greater percentage of the other face in the morph). **Notably, the self-dependent facilitation effect that we observed suggests that this pattern cannot be caused by a general effect of cardiac signals on performance. At the same time, our findings beg the question as to how exactly self-cues mechanistically facilitate self-other judgments at systole, as compared to diastole.**

Drawing on recent evidence that BSC arises from the integration of multisensory exteroceptive and interoceptive signals, we interpret the observed RT acceleration at systole in terms of multimodal enhancement that is driven by the presence of concurrent cardiac and visual signals. It has long been reported that, because multisensory stimuli are detected faster than unisensory stimuli (Raab, 1962), the simultaneous stimulation of two or more sensory modalities facilitates behaviour (Hershenson, 1962; Todd, 1912). In our studies, a multimodal enhancement of self-recognition can potentially occur only between (exteroceptive) visual information about self and (interoceptive) cardiac signals at Systole condition. Indeed, no cardiac signal is available for integration at Diastole condition. However, this hypothesis does not explain the fact that the systole-related effect we found for the self faces was still stronger at morphing levels closer to the individual PSE. Moreover, the multisensory enhancement interpretation does not take into account prior evidence of general baroreceptor-mediated inhibitory influence on subcortical and cortical activity (Dembowsky & Seller, 1995; Elbert & Raau, 1995).

Investigations of cardiac effects on visual selection efficiency may help fill this gap. Recently, Pramme and colleagues (2016) asked participants to classify target letters embedded within distractors, presented at systole or diastole. They found enhanced selection efficiency for stimuli aligned to systole, as compared to diastole. This result was also in line with prior evidence from the same group (Pramme et al., 2014) showing less mask interference during a visual masking task when mask and target are presented at systole, as compared to diastole. Interestingly, effective performance in both tasks crucially requires "noise suppression", that is, the selection of relevant information in spite of interference imposed by distracting input. This is often argued to be achieved by simultaneous excitation of pathways processing the relevant input and inhibition of pathways concerned with input that are irrelevant ("noise") for the ongoing task (e.g., (Duncan, Humphreys, & Ward, 1997; Wuhr & Frings, 2008)). Starting from this model, in order to explain their results, Pramme and colleagues (2016) proposed that the general baroreceptor-mediated inhibition during systole might facilitate selection of target stimuli through the suppression of neural activity related to noisy, irrelevant information. Something similar might occur in our study especially when the "noise" (i.e., the amount of morphing) is added to the self-face, that is, when the alignment of the attentional focus to self-cues is more difficult. At these conditions, facilitation (i.e. RTs acceleration) of self-other judgments during systole, as compared to diastole, might depend upon baroreceptor-mediated inhibition, which would bolster attention to task-relevant information ("self-cues") by withdrawing activity from the brain structures that are currently processing interfering input (i.e., other-cues). In sum, an interaction between the specific bias to attend self-related stimuli (Sui & Humphreys, 2017) and the baroreceptor-mediated modulation of visual selection efficiency (Pramme et al., 2016) would explain cardiac effects on self-other recognition. However, despite the increasing evidence that response inhibition enabling better performance improves at systole (e.g. during a stop-signal task; (Rae et al., 2018)), it should be noticed that a different explanation is also possible, that is, one based on the relative enhancement of relevant cues. From this perspective, cardiac signals would enhance visual processing of relevant information rather than inducing inhibition of irrelevant ones. For instance, Ronchi et al. (2017) investigated the impact of cardiac signals on the neural processing of body images. They found that cardiac

signals enhance two prominent steps of visual information processing: an early period that has been linked to the first categorization of the image and a later component that is relevant for processing of complex stimuli, such as faces and bodies. Research is at too early a stage to draw definitive conclusions on this regard. Lastly, the possibility that faster self-other judgments at more ambiguous (or "noisy") conditions may reflect an effect of internal bodily states on the feeling of confidence guiding them (Allen et al., 2016) is something to be clarified in future investigations too. **It is worth reiterating that our results (specifically, the significant 3-way interactions we observed across both experiments) indicate that – at least in the task we employed here – the baroreceptor input specifically affected self-processing, rather than inducing a general alteration in the performance speed.**

Beyond the specific effects of baroreceptor firing on self-recognition, we also observed (in Study 1) a positive correlation between self-bias and IAcc, a pattern that was independent of the cardiac cycle effect. In other words, participants with higher IAcc values showed a bias towards judging the stimuli as self. This finding probably reflects a trait-like effect of interoception on the processing of self-related stimuli, comparable to the ones reported in recent studies that have used self-like stimuli to investigate the role of interoception for BSC (Aspell et al., 2013; Suzuki et al., 2013). In Suzuki et al (2013) participants with higher IAcc experienced a stronger sense of ownership over the seen hand (Suzuki et al., 2013). It seems that when exposed to stimuli that resemble the self, higher levels of IAcc may facilitate identification with that stimulus (see also (Sel et al., 2017)), whereas under conditions where the stimulus may be alien to the self, such as in the rubber hand illusion, the interoceptive cues of the individuals with higher heartbeat perception may serve to anchor them in their own bodies and disrupt the identification with non-self stimuli. As has been previously suggested, for higher IAcc the brain weights interoceptive predictions and prediction errors as more reliable (Ainley, Apps, Fotopoulou, & Tsakiris, 2016). In the context of the present experiment, as was also the case in past studies that used self-like stimuli (Aspell et al., 2013; Sel et al., 2017; Suzuki et al., 2013), the interoceptive cues indicate that the seen hand or face is one's own because its visual appearance is congruent with the individual's continually updating of interoceptive priors while perceiving one's self. However, as shown here, this

effects seems to be independent from the effects of spontaneous cardiac afferent signals, suggesting that the effect of interoceptive accuracy on self-representations may reflect longer-term and more stable trait-like influences on self-processing.

The present findings have interesting implications for our understanding of the nature of disturbances of self-experience, which can be characterized by a varying degree of depersonalization, i.e., having the impression of seeing another "identity" than oneself in the mirror. Interestingly, depersonalization phenomenology seems to engage impaired processing of interoceptive body signaling (Sedeno et al., 2014). In particular, anomalies of subjective experience (e.g., (Nelson, Parnas, & Sass, 2014; Raballo, Saebye, & Parnas, 2011; Sass & Parnas, 2003)) and bodily self representations (Ardizzi et al., 2016; Di Cosmo et al., 2017; Ferri, Ambrosini, & Costantini, 2016; Ferri et al., 2014; Ferri et al., 2012; Gallese & Ferri, 2014) have been suggested to be central features of schizophrenia spectrum conditions. Relevant to our study, patients with schizophrenia (Caputo et al., 2012) as well as individuals reporting schizotypal traits (Fonseca-Pedrero et al., 2015) are also more prone to experimentally induced self-face illusions. In addition to schizophrenia spectrum conditions, depersonalization is also a prominent symptom in other non-dissociative disorders, such as borderline personality disorder (BDP (Vermetten & Spiegel, 2014)). Interestingly, central-cardiac coupling and cortical representation of cardiac signals seem to be altered in schizophrenia (Schulz, Bolz, Bar, & Voss, 2016) and BDP (Muller et al., 2015). Based on our results, it is reasonable to hypothesize that this may negatively affect cardiac modulation of self-other recognition and, thus, contribute to specific depersonalization symptoms in these mental disorders. Further research is needed in order to investigate the central-cardiac coupling and its impact on self-identity in individuals with specific disturbances of self-experience.

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References

Ainley, V., Apps, M. A., Fotopoulou, A., & Tsakiris, M. (2016). 'Bodily precision': a predictive coding account of individual differences in interoceptive accuracy. *Philos Trans R Soc Lond B Biol Sci, 371*(1708). doi: 20160003 [pii]10.1098/rstb.2016.0003rstb.2016.0003 [pii]

Allen, M., Frank, D., Schwarzkopf, D. S., Fardo, F., Winston, J. S., Hauser, T. U., & Rees, G. (2016). Unexpected arousal modulates the influence of sensory noise on confidence. *Elife, 5*. doi: 10.7554/eLife.18103e18103 [pii]

Ambrosini, E., Pezzulo, G., & Costantini, M. (2015). The eye in hand: predicting others' behavior by integrating multiple sources of information. *J Neurophysiol, 113*(7), 2271-2279. doi: 10.1152/jn.00464.2014jn.00464.2014 [pii]

Ardizzi, M., Ambrosecchia, M., Buratta, L., Ferri, F., Peciccia, M., Donnari, S., . . . Gallese, V. (2016). Interoception and Positive Symptoms in Schizophrenia. *Front Hum Neurosci, 10*, 379. doi: 10.3389/fnhum.2016.00379

Aspell, J. E., Heydrich, L., Marillier, G., Lavanchy, T., Herbelin, B., & Blanke, O. (2013). Turning body and self inside out: visualized heartbeats alter bodily self-consciousness and tactile perception. *Psychol Sci, 24*(12), 2445-2453. doi: 10.1177/0956797613498395095679761349839509567976134983950956797613498395 [pii]

Azevedo, R. T., Badoud, D., & Tsakiris, M. (2017). Afferent cardiac signals modulate attentional engagement to low spatial frequency fearful faces. *Cortex*. doi: S0010-9452(17)30205-8 [pii]10.1016/j.cortex.2017.06.016

Azevedo, R. T., Garfinkel, S. N., Critchley, H. D., & Tsakiris, M. (2017). Cardiac afferent activity modulates the expression of racial stereotypes. *Nat Commun, 8*, 13854. doi: 10.1038/ncomms13854ncomms13854 [pii]

Baayen, R. H., Davidson, D. J., & Bates, D. M. (2008). Mixed-effects modeling with crossed random effects for subjects and items. *Journal of Memory and Language, 59*(4), 390-412.

Bates, D., Mächler, M., Bolker, B., & Walker, S. (2015). Fitting Linear Mixed-Effects Models Using lme4. *Journal of Statistical Software, 67*(1), 1-48.

Bird, G., & Viding, E. (2014). The self to other model of empathy: providing a new framework for understanding empathy impairments in psychopathy, autism, and alexithymia. *Neurosci Biobehav Rev, 47*, 520-532. doi: S0149-7634(14)00257-7 [pii]10.1016/j.neubiorev.2014.09.021

Blanke, O. (2012). Multisensory brain mechanisms of bodily self-consciousness. *Nat Rev Neurosci, 13*(8), 556-571. doi: 10.1038/nrn3292nrn3292 [pii]

Caputo, G. B., Ferrucci, R., Bortolomasi, M., Giacopuzzi, M., Priori, A., & Zago, S. (2012). Visual perception during mirror gazing at one's own face in schizophrenia. *Schizophr Res, 140*(1-3), 46-50. doi: 10.1016/j.schres.2012.06.029S0920-9964(12)00346-5 [pii]

Craig, A. D. (2002). How do you feel? Interoception: the sense of the physiological condition of the body. *Nat Rev Neurosci, 3*(8), 655-666. doi: 10.1038/nrn894nrn894 [pii]

Craig, A. D. (2003). Interoception: the sense of the physiological condition of the body. *Curr Opin Neurobiol, 13*(4), 500-505. doi: S0959438803000904 [pii]

Critchley, H. D., & Harrison, N. A. (2013). Visceral influences on brain and behavior. *Neuron, 77*(4), 624-638. doi: 10.1016/j.neuron.2013.02.008S0896-6273(13)00140-2 [pii]

Dembowsky, K., & Seller, H. (1995). Arterial baroreceptor reflexes. In D. a. S. Vaitl, R (Ed.), *From the heart to the brain: The psychophysiology of circulation-brain interaction* (pp. 35-60). Frankfurt, Germany: Peter Lang.

Di Cosmo, G., Costantini, M., Salone, A., Martinotti, G., Di Iorio, G., Di Giannantonio, M., & Ferri, F. (2017). Peripersonal space boundary in schizotypy and schizophrenia. *Schizophr Res*. doi: S0920-9964(17)30755-7 [pii]10.1016/j.schres.2017.12.003

Duncan, J., Humphreys, G., & Ward, R. (1997). Competitive brain activity in visual attention. *Curr Opin Neurobiol, 7*(2), 255-261. doi: S0959-4388(97)80014-1 [pii]

Elbert, T., & Raau, H. (1995). What goes up (from heart to brain) must calm down (frombrain to heart)! Studies on the interaction between baroreceptor activity andcortical excitability. In D. a. S. Vaitl, R

(Ed.), *From the heart to the brain:The psychophysiology of circulation–brain interaction* (pp. 133-149). Frankfurt, Germany: Peter Lang.

Ferri, F., Ambrosini, E., & Costantini, M. (2016). Spatiotemporal processing of somatosensory stimuli in schizotypy. *Sci Rep, 6*, 38735. doi: 10.1038/srep38735srep38735 [pii]

Ferri, F., Costantini, M., Salone, A., Di Iorio, G., Martinotti, G., Chiarelli, A., . . . Gallese, V. (2014). Upcoming tactile events and body ownership in schizophrenia. *Schizophr Res, 152*(1), 51-57. doi: 10.1016/j.schres.2013.06.026S0920-9964(13)00326-5 [pii]

Ferri, F., Frassinetti, F., Mastrangelo, F., Salone, A., Ferro, F. M., & Gallese, V. (2012). Bodily self and schizophrenia: the loss of implicit self-body knowledge. *Conscious Cogn, 21*(3), 1365-1374. doi: 10.1016/j.concog.2012.05.001S1053-8100(12)00130-4 [pii]

Fiacconi, C. M., Peter, E. L., Owais, S., & Kohler, S. (2016). Knowing by heart: Visceral feedback shapes recognition memory judgments. *J Exp Psychol Gen, 145*(5), 559-572. doi: 10.1037/xge00001642016-15302-001 [pii]

Fonseca-Pedrero, E., Badoud, D., Antico, L., Caputo, G. B., Eliez, S., Schwartz, S., & Debbane, M. (2015). Strange-face-in-the-mirror illusion and schizotypy during adolescence. *Schizophr Bull, 41 Suppl 2*, S475-482. doi: 10.1093/schbul/sbu196sbu196 [pii]

Gallese, V., & Ferri, F. (2014). Psychopathology of the bodily self and the brain: the case of schizophrenia. *Psychopathology, 47*(6), 357-364. doi: 10.1159/000365638000365638 [pii]

Garfinkel, S. N., Barrett, A. B., Minati, L., Dolan, R. J., Seth, A. K., & Critchley, H. D. (2013). What the heart forgets: Cardiac timing influences memory for words and is modulated by metacognition and interoceptive sensitivity. *Psychophysiology, 50*(6), 505-512. doi: 10.1111/psyp.12039

Garfinkel, S. N., Minati, L., Gray, M. A., Seth, A. K., Dolan, R. J., & Critchley, H. D. (2014). Fear from the heart: sensitivity to fear stimuli depends on individual heartbeats. *J Neurosci, 34*(19), 6573-6582. doi: 10.1523/JNEUROSCI.3507-13.201434/19/6573 [pii]

Gray, M. A., Beacher, F. D., Minati, L., Nagai, Y., Kemp, A. H., Harrison, N. A., & Critchley, H. D. (2012). Emotional appraisal is influenced by cardiac afferent information. *Emotion, 12*(1), 180-191. doi: 10.1037/a00250832011-23008-001 [pii]

Hershenson, M. (1962). Reaction time as a measure of intersensory facilitation. *J Exp Psychol, 63*, 289-293.

Heydrich, L., Aspell, J. E., Marillier, G., Lavanchy, T., Herbelin, B., & Blanke, O. (2018). Cardio-visual full body illusion alters bodily self-consciousness and tactile processing in somatosensory cortex. *Sci Rep, 8*(1), 9230. doi: 10.1038/s41598-018-27698-210.1038/s41598-018-27698-2 [pii]

Keenan, J. P., McCutcheon, B., Freund, S., Gallup, G. G., Jr., Sanders, G., & Pascual-Leone, A. (1999). Left hand advantage in a self-face recognition task. *Neuropsychologia, 37*(12), 1421-1425. doi: S0028-3932(99)00025-1 [pii]

Kliegl, R., Wei, P., Dambacher, M., Yan, M., & Zhou, X. (2010). Experimental Effects and Individual Differences in Linear Mixed Models: Estimating the Relationship between Spatial, Object, and Attraction Effects in Visual Attention. *Front Psychol, 1*, 238. doi: 10.3389/fpsyg.2010.00238

Montefinese, M., Zannino, G. D., & Ambrosini, E. (2015). Semantic similarity between old and new items produces false alarms in recognition memory. *Psychol Res, 79*(5), 785-794. doi: 10.1007/s00426-014-0615-z

Muller, L. E., Schulz, A., Andermann, M., Gabel, A., Gescher, D. M., Spohn, A., . . . Bertsch, K. (2015). Cortical Representation of Afferent Bodily Signals in Borderline Personality Disorder: Neural Correlates and Relationship to Emotional Dysregulation. *JAMA Psychiatry, 72*(11), 1077-1086. doi: 10.1001/jamapsychiatry.2015.12522436270 [pii]

Nelson, B., Parnas, J., & Sass, L. A. (2014). Disturbance of minimal self (ipseity) in schizophrenia: clarification and current status. *Schizophr Bull, 40*(3), 479-482. doi: 10.1093/schbul/sbu034sbu034 [pii]

Park, H. D., Bernasconi, F., Bello-Ruiz, J., Pfeiffer, C., Salomon, R., & Blanke, O. (2016). Transient Modulations of Neural Responses to Heartbeats Covary with Bodily Self-Consciousness. *J Neurosci, 36*(32), 8453-8460. doi: 10.1523/JNEUROSCI.0311-16.201636/32/8453 [pii]

Pernet, C. R., Wilcox, R., & Rousselet, G. A. (2012). Robust correlation analyses: false positive and power validation using a new open source matlab toolbox. *Front Psychol, 3*, 606. doi: 10.3389/fpsyg.2012.00606

Pfeifer, G., Garfinkel, S. N., Gould van Praag, C. D., Sahota, K., Betka, S., & Critchley, H. D. (2017). Feedback from the heart: Emotional learning and memory is controlled by cardiac cycle, interoceptive accuracy and personality. *Biol Psychol, 126*, 19-29. doi: S0301-0511(17)30058-3 [pii]10.1016/j.biopsycho.2017.04.001

Pramme, L., Larra, M. F., Schachinger, H., & Frings, C. (2014). Cardiac cycle time effects on mask inhibition. *Biol Psychol, 100*, 115-121. doi: 10.1016/j.biopsycho.2014.05.008S0301-0511(14)00107-0 [pii]

Pramme, L., Larra, M. F., Schachinger, H., & Frings, C. (2016). Cardiac cycle time effects on selection efficiency in vision. *Psychophysiology, 53*(11), 1702-1711. doi: 10.1111/psyp.12728

Quené, H., & van den Bergh, H. (2008). Examples of mixed-effects modeling with crossed random effects and with binomial data. *Journal of Memory and Language, 59*(4), 413-425.

Raab, D. H. (1962). Statistical facilitation of simple reaction times. *Trans N Y Acad Sci, 24*, 574-590.

Raballo, A., Saebye, D., & Parnas, J. (2011). Looking at the schizophrenia spectrum through the prism of self-disorders: an empirical study. *Schizophr Bull, 37*(2), 344-351. doi: 10.1093/schbul/sbp056sbp056 [pii]

Rae, C. L., Botan, V. E., Gould van Praag, C. D., Herman, A. M., Nyyssonen, J. A. K., Watson, D. R., . . . Critchley, H. D. (2018). Response inhibition on the stop signal task improves during cardiac contraction. *Sci Rep, 8*(1), 9136. doi: 10.1038/s41598-018-27513-y10.1038/s41598-018-27513-y [pii]

RCoreTeam. (2017). R: A language and environment for statistical computing, from https://http://www.R-project.org/

Ronchi, R., Bernasconi, F., Pfeiffer, C., Bello-Ruiz, J., Kaliuzhna, M., & Blanke, O. (2017). Interoceptive signals impact visual processing: Cardiac modulation of visual body perception. *Neuroimage, 158*, 176-185. doi: S1053-8119(17)30535-9 [pii]10.1016/j.neuroimage.2017.06.064

Salomon, R., Ronchi, R., Donz, J., Bello-Ruiz, J., Herbelin, B., Martet, R., . . . Blanke, O. (2016). The Insula Mediates Access to Awareness of Visual Stimuli Presented Synchronously to the Heartbeat. *J Neurosci, 36*(18), 5115-5127. doi: 10.1523/JNEUROSCI.4262-15.201636/18/5115 [pii]

Sass, L. A., & Parnas, J. (2003). Schizophrenia, consciousness, and the self. *Schizophr Bull, 29*(3), 427-444.

Schandry, R. (1981). Heart Beat Perception and Emotional Experience. *Psychophysiology, 18*(4), 483-488.

Schulz, S., Bolz, M., Bar, K. J., & Voss, A. (2016). Central- and autonomic nervous system coupling in schizophrenia. *Philos Trans A Math Phys Eng Sci, 374*(2067). doi: 10.1098/rsta.2015.017820150178 [pii]

Sedda, A., Ambrosini, E., Dirupo, G., Tonin, D., Valsecchi, L., Redaelli, T., . . . Bottini, G. (2018). Affordances after spinal cord injury. *J Neuropsychol*. doi: 10.1111/jnp.12151

Sedeno, L., Couto, B., Melloni, M., Canales-Johnson, A., Yoris, A., Baez, S., . . . Ibanez, A. (2014). How do you feel when you can't feel your body? Interoception, functional connectivity and emotional processing in depersonalization-derealization disorder. *PLoS One, 9*(6), e98769. doi: 10.1371/journal.pone.0098769PONE-D-13-53968 [pii]

Sel, A., Azevedo, R. T., & Tsakiris, M. (2017). Heartfelt Self: Cardio-Visual Integration Affects Self-Face Recognition and Interoceptive Cortical Processing. *Cereb Cortex, 27*(11), 5144-5155. doi: 10.1093/cercor/bhw2963056463 [pii]

Seth, A. K., & Tsakiris, M. (2018). Being a Beast Machine: The Somatic Basis of Selfhood. *Trends Cogn Sci, 22*(11), 969-981. doi: S1364-6613(18)30207-9 [pii]10.1016/j.tics.2018.08.008

Sui, J., & Humphreys, G. W. (2017). The ubiquitous self: what the properties of self-bias tell us about the self. *Ann N Y Acad Sci, 1396*(1), 222-235. doi: 10.1111/nyas.13197

Suzuki, K., Garfinkel, S. N., Critchley, H. D., & Seth, A. K. (2013). Multisensory integration across exteroceptive and interoceptive domains modulates self-experience in the rubber-hand illusion. *Neuropsychologia, 51*(13), 2909-2917. doi: 10.1016/j.neuropsychologia.2013.08.014S0028-3932(13)00278-9 [pii]

Tajadura-Jimenez, A., & Tsakiris, M. (2014). Balancing the "inner" and the "outer" self: interoceptive sensitivity modulates self-other boundaries. *J Exp Psychol Gen, 143*(2), 736-744. doi: 10.1037/a00331712013-19665-001 [pii]

Todd, J. (1912). *Reaction to multiple stimuli*. New York: Science Press.

Tsakiris, M., & De Preester, H. (2018). *The Interoceptive Mind: From Homeostasis to Awareness* Oxford University Press.

Tsakiris, M., Tajadura-Jiménez, A., & Costantini, M. (2011). Just a heartbeat away from one's body: interoceptive sensitivity predicts malleability of body-representations. *Proceedings of the Royal Society B: Biological Sciences, 278*(1717), 2470-2476. doi: 10.1098/rspb.2010.2547

Vermetten, E., & Spiegel, D. (2014). Trauma and dissociation: implications for borderline personality disorder. *Curr Psychiatry Rep, 16*(2), 434. doi: 10.1007/s11920-013-0434-8

Wuhr, P., & Frings, C. (2008). A case for inhibition: visual attention suppresses the processing of irrelevant objects. *J Exp Psychol Gen, 137*(1), 116-130. doi: 10.1037/0096-3445.137.1.1162008-01081-008 [pii]